ORYCTOCEPHALID TRILOBITES FROM THE CAMBRIAN OF NORTH AMERICA

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ABSTRACT. Type and additional specimens of species of *Oryctocephalus*, *Lancastria* and *Oryctocara* are described. Oryctocephalidae have a rostral-hypostomal plate, and hence belong in the Order Corynexochida. Characteristic of the family is the development of lateral glabellar furrows as pits situated inside the axial furrow, and the absence of a border on the pygidium. Two subfamilies are used: Oryctocephalinae, having genal and pleural spines; Oryctocarinae lacking such spines. Species of both groups are found in late Lower to mid Middle Cambrian rocks of North America, Siberia, Asia and Australia, and rare examples occur in South America and Antarctica. Oryctocephalids are typical of deposits in outer shelf and slope areas, in which completely or partially articulated exoskeletons are characteristic. Arrangements of sclerites in such specimens of *Oryctocephalus burgessensis* are considered to result from burial events, not from manoeuvres during exuviation. Compaction and tectonic distortion of specimens in these fine-grained clastic rocks renders questionable some of the characters used in taxonomy.

NEW specimens and the types of two rare oryctocephalids, *Lancastria roddyi* (Lower Cambrian) and *Oryctocara geikiei* (Middle Cambrian), are described, together with the type and additional specimens of *Oryctocephalus reynoldsi*, and well-preserved examples of *O. burgessensis* (both Middle Cambrian). These species of three genera epitomize the morphological range encompassed by the family. The hallmark of an oryctocephalid, as Raymond (1913, p. 716) recognized, is that the glabella had an occipital furrow, and three or four lateral glabellar furrows, each in the form of a pit situated a short distance inside the axial furrow.

Oryctocephalids are found in North America in outer shelf or slope deposits, not in platform sites (Fritz 1990, p. 108). From the late Lower Cambrian *Oleuellus* Zone species of *Lancastria*, *Goldfieldia* and *Arthricocephalus* have been described, and *Changaspis* and *Ovatoryctocara* recorded. In the Middle Cambrian species of *Oryctocephalus* (and those referred to *Oryctocephalites* or *Oryctocephalina*) and *Oryctocara* are known from the interval spanning the *Plagiura-Poliella* to *Bathyuriscus-Elrathina* zones. In the overlying *Ptychagnostus gibbus* Zone (mid Middle Cambrian) the last oryctocephalid, *Tonkinella*, is present. The stratigraphical ranges of species of different genera of oryctocephalids in the Middle Cambrian thus comprise the range of the *Oryctocephalus* Zone in the outer shelf facies (Robison 1976, p. 101, text-fig. 5). In Siberia, eastern Asia, Australia, Antarctica and Argentina (Shergold 1969, text-fig. 2) oryctocephalids are found in Lower and Middle Cambrian rocks of similar facies and range in time. This geographical distribution is independent of the Lower Cambrian olenellid and redlichiid faunal realms (Fortey and Owens 1990, p. 144, fig. 7.2) as is that of the peculiar *Bathynotus* (Whittington 1988, p. 581; Zhao *et al.* 1990). In the Middle Cambrian, burlingiids (Whittington 1994) have a distribution similar to that of oryctocephalids, but also occur in Sweden. Cambrian palaeogeography (Scotese and McKerrow 1990, figs 3–4) points to the isolation of Baltica in high latitudes as having influenced these distributions.

Oryctocephalidae are characteristic of outer shelf sites, many specimens being preserved in fine-grained clastic rocks, and hence flattened; the considerable convexity of the rare limestone preservation of cranidia was described by Fritz (1968, pl. 40, figs 14–16; pl. 41, figs 9–11, 25–27) and Shergold (1969, text-fig. 9). In outer shelf and slope sites, however, articulated dorsal exoskeletons are more commonly found than in open shelf deposits (cf. Fortey 1975; Taylor 1976), so

that the type species of many genera are known from such examples, which may, or may not, have the free cheeks attached. The results of compaction on the outline and lobation of the glabella, and the effects of tectonic distortion, make distinctions between species difficult, either in material from the same or different geographical areas (cf. Shergold 1969, p. 28). They also make questionable the validity of certain characters used in distinctions between genera. For example, is the 'quilted' appearance (Lermontova *in* Vologdin 1940, p. 137) of glabellar lobation, or the sinuosity of the axial furrows in relation to these lobes (used by Shergold 1969, p. 48, in characterizing *Oryctocephalina*) original or partially or wholly the result of flattening a convex cranidium?

Rasetti (*in* Moore 1959, p. O219) included six genera in the Oryctocephalidae, and doubtfully *Cheiruroides* (regarded subsequently as a member of a separate family of Corynexochida by Chang 1963). Rasetti (1952) had earlier described the rostral-hypostomal plate in *Oryctocephalus*, and included this feature, and the lack of a border in the pygidium, as characters of oryctocephalids. He ignored the subfamilies established by Hupé (1953, p. 186; 1955, p. 111) who recognized the two different types of oryctocephalids described herein. These are the *Oryctocephalus* type, having the genal spine and pleural spines on thorax and pygidium, and the *Oryctocara* type, lacking such spines. Hupé also recognized (with question) a third subfamily, to include *Tonkinella* Mansuy, 1916, with its five thoracic segments and short pygidial axis. Chang (1980), in addition to using these three subfamilies, used Lancastriinae Kobayashi, 1935, to include *Lancastria* and other genera. Since 1960 new genera based on Siberian material have been erected, and additional new genera for Chinese Lower and Middle Cambrian species. In Zhang *et al.* (1980) a more elaborate classification is used, which raises oryctocephalids to superfamily rank, and recognizes the spine-bearing and non-spinose forms as separate families, each ranging from Lower to Middle Cambrian. Here I revert to using a single family, with the two subfamilial divisions first recognized by Hupé, because the available information on morphology does not appear to provide diagnostic characters for further subdivision. I attempt here, for brevity, to give in a diagnosis only distinctive, cardinal characters; such characters are not repeated in a diagnosis at a lower taxonomic rank.

Oryctocephalids were placed in the Order Corynexochida in Moore (1959) and by Öpik (1982, p. 6). The protaspis of *Bathyuriscus* (Robison 1967; see also Fortey and Chatterton 1988, pl. 17, figs 8, 11, 12, 14–15 (not figs 7, 9–10, 13, 16–19 as given in the plate explanation, in which the names *Bathyuriscus*? and *Spencella*? have been transposed in error; B. D. E. Chatterton, pers. comm.), text-fig. 10, 6a–b), has the rostral plate and hypostome fused into a rostral-hypostomal plate. This plate appears to be the cardinal character of Corynexochida, and is associated with the absence of a preglabellar field in later developmental stages, so that in holaspides the frontal lobe of the glabella abuts against the anterior border. Other characters of the protaspis of *Bathyuriscus* – the forwardly-expanding glabella, the fossula, proparian suture, and marginal spines – are shared with Ptychopariida (Fortey and Chatterton 1988, text-fig. 10, figs 7a–b, 8a–b). In Ptychopariida the rostral plate and hypostome are separated by the hypostomal suture in the protaspis, and during meraspid development the hypostome becomes natant as a preglabellar field develops. In the meraspid development of Corynexochida (Suvorova 1964, text-fig. 74; Robison 1967; Öpik 1982) intergenal spines may be present, but this is a character shared with Olenellina (Palmer 1957) and Paradoxidoidea (Whittington 1957, fig. 5). Thus, while Robison (1967) first drew attention to the similarities between earliest known developmental stages in Ptychopariida and Corynexochida, the two groups appear to be distinct – the former developing a natant hypostome, the latter retaining from the earliest stage a rostral-hypostomal plate.

SYSTEMATIC PALAEONTOLOGY

Family ORYCTOCEPHALIDAE Beecher, 1897

Diagnosis. If the Order Corynexochida is characterized as having the rostral-hypostomal plate present in the smallest known protaspid, and retained into the holaspid stage (and lacking a preglabellar field), then the Oryctocephalidae may be diagnosed as having the glabella with SO

complete, transverse, S1–3 or 4 in the form of pits situated a short distance inside the axial furrow. In many species a pit is developed close to the outer end of the occipital furrow, and a pit is similarly situated in the articulating furrow; thus paired axial apodemes, most conspicuous in the glabella, appear to be characteristic. The pygidium lacks a convex or smooth border, pleural and interpleural furrows extend to the margin; doublure narrow and gently convex.

Stratigraphical range. In North America oryctocephalids appear first in the high Lower Cambrian *Olenellus* Zone. The youngest known appears to be a species of *Tonkinella* (Fritz 1971, p. 1168, figs 4, 6) in a deeper water faunule with agnostids at the base of the Eldon Formation. Higher in the Eldon Formation is the Black Band, the fauna of which (Robison 1984, p. 6) is that of the *Ptychagnostus gibbus* Zone. Faunas in Eastern Asia (Chang 1988) include oryctocephalids spanning a comparable range, species of *Tonkinella* being the youngest and occurring at a similar level to that in North America. In the north-east part of the Siberian platform, in the transition to, and in the marine argillaceous facies, oryctocephalids occur throughout the early Middle Cambrian Amgan Stage. Earliest appearing, with paradoxidids, are *Oryctocephalops frischenfeldi* and species of *Ovatoryctocara* and *Oryctocara* (Egorova *et al.* 1976, p. 27, pls 43–46; Astashkin *et al.* 1991, pp. 74, 78, 82), with species of *Oryctocephalus* appearing at this level and higher in the stage (Egorova *et al.* 1976, p. 28, pls 47–53; Astashkin *et al.* 1991, p. 73). In the highest part of the Amgan Stage Astashkin *et al.* (1991, p. 68) record species of *Tonkinella* occurring with *Ptychagnostus gibbus*, *Tomagnostus fissus* and *Paradoxides sacheri*. Thus species of *Tonkinella* appear to be everywhere the youngest oryctocephalids.

Remarks. The North American material illustrated herein shows that there were two groups of oryctocephalids. One, typified by species of *Oryctocephalus*, had a genal spine, a spine on the end of each thoracic pleura, and marginal pygidial pleural spines. *Oryctocara* exemplifies species in which there were no marginal exoskeletal spines, and a granulate sculpture. Species of the same two groups have been recognized in Siberia by Russian authors (Lermontova, *in* Vologdin 1940; Tchernysheva 1962; Suvorova 1964), in Australia (Shergold 1969) and in China (e.g. Zhang *et al.* 1980). These two widespread branches of the oryctocephalids are regarded as subfamilies. *Lancastria* is placed in the spinose group, not in a separate subfamily. The position of the long-known *Tonkinella* Mansuy, 1916, species of which are widely distributed (Rasetti 1951, p. 196, pl. 31, figs 13–18; Kindle 1982, p. 10, pl. 1.1, figs 8, 12; Young and Ludvigsen 1989, p. 20, pl. 6, figs 5–11; fig. 6B; Reed 1934, p. 9, pl. 1, figs 3–8, 9?, 10; Tchernysheva 1962, p. 27, pl. 3, figs 1–6), is uncertain. Hupé (1953, p. 186) placed it with question in a separate subfamily, referring to the pygidium, which has a relatively short axis, lacks interpleural furrows, and hence has a radiating arrangement of pleural furrows. Pleural and marginal pygidial spines appear to be absent, but Rasetti (1951, pl. 31, fig. 14) shows a long genal spine, extending beyond the pygidium in his restoration (Rasetti, *in* Moore 1959, fig. 162,6). I therefore prefer to place *Tonkinella* in the spinose group of oryctocephalids, although it lacks pleural spines. McNamara (1986, p. 138, fig. 9) suggested that a paedomorphic reduction in the number of thoracic segments in Middle Cambrian oryctocephalids led to *Tonkinella*; this reduction being accompanied by an increase in relative size of the pygidium, loss of pleural spines, and a decrease in width (tr.) of the free cheek. McNamara also doubted that *Thoracocare* Robison and Campbell, 1974, a progenetic Corynexochida, should be assigned to the Oryctocephalidae, and I share this view. Shergold (1969, p. 56) placed his new genus *Barkleyella* in the Tonkinellinae, but only small cranidia are known, so that its position in the present classification is uncertain.

Subfamily ORYCTOCEPHALINAE Beecher, 1897

Diagnosis. Genal spine present, facial suture opisthoparian; a single spine arising from the outer end of each thoracic and pygidial pleura.

Remarks. Oryctocephalus, Oryctocephalites, Oryctocephalina, Lancastria, and *Oryctocephalops* may be placed within this subfamily, probably also *Goldfieldia* and *Tonkinella*; I do not use subfamily Lancastriinae Kobayashi, 1935 (p. 129). The Lower Cambrian *Protoryctocephalus* (Zhang *et al.* 1980, p. 270, pl. 91, fig. 1) clearly belongs here also, but *Oryctocephaloides* (Zhang *et al.* 1980, p. 271,

pl. 96, figs 5–8) has S1 continuous and S2 and S3 faint, and lacks the characteristic oryctocephalid pits. The Lower and Middle Cambrian *Oryctometopus* (Suvorova 1964, p. 252, pl. 29, figs 8–11, text-fig. 75) is known primarily from the cranidium, so that its relationships are uncertain.

<p style="text-align:center">Genus ORYCTOCEPHALUS Walcott, 1886</p>

Type species. Oryctocephalus primus Walcott, 1886.

Diagnosis. Glabella parallel-sided or expanded slightly forward to a maximum anterior width, S1–3 deep pits, S1 pits connected by shallow transverse furrow, S2 and S3 pits may be connected by furrows successively shallower forwards, S4 pits small, faint; anterior margin of rostral-hypostomal plate slightly wider (tr.) than maximum glabellar width. Thorax of seven segments, pygidium with five or six pairs of pleurae.

Remarks. Oryctocephalus reynoldsi is the most completely known species, recognized world-wide, and the diagnosis is based largely upon it. The type species, known only from detached cranidia and pygidia, was redescribed by Palmer (1954, p. 68, pl. 15, figs 1–2; the pygidium by Shergold 1969, p. 15, text-fig. 4) and is from the Middle Cambrian, Pioche Formation, Pioche, Nevada. Fritz (1968, p. 201, pl. 40, figs 14–16) described a damaged cranidium from limestone in the *Albertella* Zone, which retained some convexity, and compared it with *O. primus*.

Oryctocephalites typicalis Resser, 1939*b* (p. 44, pl. 3, figs 1–6; holotype cranidium designated p. 66) is from the 'Langston' Limestone, Wasatch Mountains, Idaho. It is known only from isolated cranidia and pygidia (see Fritz 1968, p. 202, pl. 41, figs 9–11; Shergold 1969, text-fig. 9; Palmer and Halley 1979, p. 84, pl. 13, figs 1–4), and is said to be distinguished from *Oryctocephalus* by the more oval glabellar outline, the maximum width being at a level between S2 and S3; the pygidium has five pairs of pleurae. Shergold (1969, p. 17) sought to characterize *Oryctocephalites* by the pygidium having only five segments, but Palmer and Halley (1979, p. 83) did not accept this. These latter authors stated that in *Oryctocephalites* only the S1 pits are connected by a shallow transverse furrow, whereas in *Oryctocephalus* at least the S1 and S2 pits are connected by transverse furrows. In flattened material such a distinction would be difficult to apply. Until more complete specimens of the species concerned are described, use of the name *Oryctocephalites* will remain problematical.

Oryctocephalina reticulata Lermontova, 1940 (*in* Vologdin 1940, p. 137, pl. 42, figs 3, 3a–b) is the type species of a genus supposedly distinguished by the sinuous course of the axial furrows around inflated portions of the glabella outside pits S1–3. This character is shown in the flattened cranidia illustrated by Tchernysheva (1962, pl. 2, figs 1–8) and by Shergold (1969, pl. 11, figs 2–3; pl. 12, fig. 4). Whether such features result from flattening of a convex cranidium, or are original, is uncertain. Palmer and Halley (1979, p. 83, pl. 12, figs 21–22, 27) use this generic name with question for

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<p style="text-align:center">EXPLANATION OF PLATE 1</p>

Figs 1, 3–6. *Oryctocephalus reynoldsi* Reed, 1899. Middle Cambrian, Stephen Formation, British Columbia, Canada. 1, SM A1425, holotype, north-west slope, Mt Stephen; dorsal view of internal mould; × 5. 3, 6, ROM 49966, Mt Stephen; external mould of exoskeleton lacking cranidium, combined with internal mould of rostral-hypostomal plate and doublure; 3, oblique view of rostral-hypostomal plate and adjacent doublure; × 10; 6, entire specimen, ventral view; × 3. 4–5, ROM 49968a, internal mould of five anterior segments and detached pygidium, combined with external mould of doublure and rostral-hypostomal plate, Mt Stephen; 4, dorsal view of portion of anterior, connective suture arrowed; × 7; 5, posterior portion of pygidium, inner edge of doublure arrowed; × 7.

Fig. 2. *Oryctocephalus burgessensis* Resser, 1938. Middle Cambrian, Burgess Shale, British Columbia, Canada. ROM 38613, talus in Walcott quarry, internal mould, pleural spines on left side bent upwards so that basal portions appear swollen; × 5.

PLATE 1
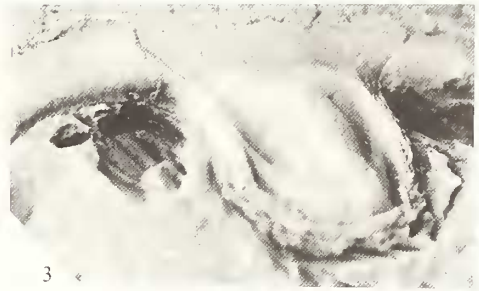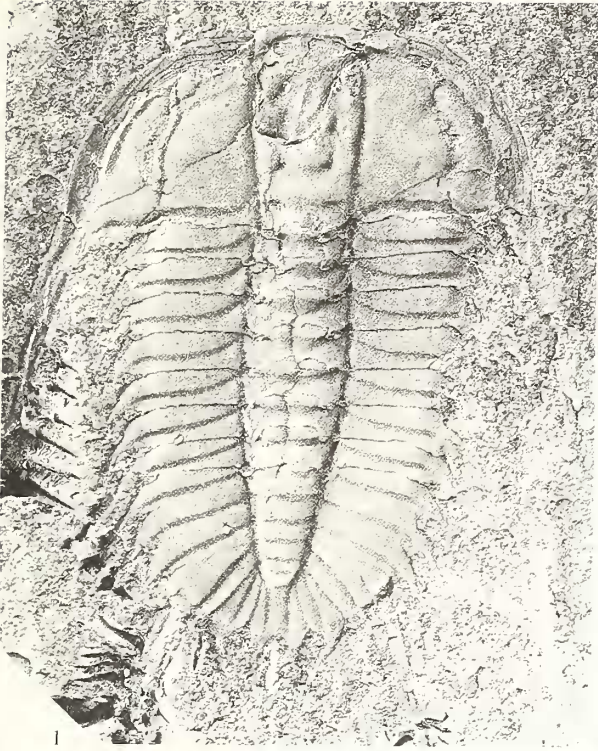
limestone cranidia retaining convexity, which show inflated outer portions of L1 and L2. Tchernysheva referred the type species *reticulata* to *Oryctocephalus*, because it was known only from cranidia. As discussed below, Shergold (1969, pl. 11, fig. 1) had an entire dorsal exoskeleton with this type of glabella, and hence referred it to *Oryctocephalina*. On the other hand, as Shergold recognized, the entire exoskeleton is strikingly like that of *Lancastria*.

Oryctocephalus reynoldsi Reed, 1899

Plate 1, figures 1, 3–6

Holotype. SM A1425, internal mould of exoskeleton in shale. In all probability Reynolds' collection (Reed 1899) came from the well-known USNM locality 14S, on the north-west side of Mt Stephen (Walcott 1908a); also locality S8d of Rasetti (1951, pp. 76, 128) and locality S of Fritz (1971, figs 1, 6). The collection contains also *Ogygopsis klotzi* (SM A1636, 1638, 1451), *Olenoides serratus* (SM A1440), *Elrathina cordillerae* (SM A1643), *Kootenia dawsoni* (SM A1424), *Bathyuriscus rotundatus* (SM A1423), and *Peronopsis montis* (SM A1644). These identifications were made following Rasetti (1951), and indicate his *O. klotzi* faunule and hence the early *Bathyuriscus-Elrathina* Zone in the Stephen Formation (Fritz 1971, p. 1164).

Other Material. USNM 116238, internal mould, original of Rasetti 1951, pl. 29, fig. 5; external mould, original of Whittington 1992, p. 125, pl. 66; Burgess Shale, Walcott quarry. ROM 49966 to 49968 inclusive, from locality 9 of Collins *et al.* (1983), which also yielded *O. geikiei*; *Glossopleura* Zone, Stephen Formation. ROM 49965, Mt Stephen.

Stratigraphical range. Stephen Formation, *Glossopleura* and *Bathyuriscus-Elrathina* zones.

Description. The holotype (Pl. 1, fig. 1) was illustrated originally only by a drawing. The exoskeleton has been flattened by compaction, compressing the glabella against the external mould of the rostral-hypostomal plate (not mentioned by Reed) and giving an irregular longitudinal infold in the thoracic axis. This compaction rotated the rostral-hypostomal plate slightly clockwise, causing the border to project on the left side in the line of the axial furrow; it also impressed the glabellar pits into the mould of the hypostome.

The glabella appears to expand slightly and evenly forward from the occipital ring to the level of the lateral border furrow, and is then rounded and abuts against the narrow (sag. and exs.) anterior border. The straight, shallow occipital furrow deepens a short distance inside the axial furrow to form an apodeme. The three pairs of deep pits, S1–3, are approximately evenly spaced from each other and the occipital furrow, and are situated a short distance inside the axial furrow. The S1 pits are joined by a shallow transverse furrow. In USNM 116238, and a large, incomplete external mould of a cranidium on ROM 49967, a smaller, shallower S4 is present, situated closer to the axial furrow and opposite the end of the eye ridge. The long, narrow (tr.) curved palpebral lobe is situated far out on the cheek, the anterior branch of the suture curving forward, the posterior directed slightly outward and backward and then curving to cross the posterior border. Eye ridge low, directed inward and forward, lying a short distance inside the lateral cephalic border. This border is wider than the anterior border, convex, underlain by the ventrally convex doublure. The doublure bears four or five strong terrace ridges running subparallel to the margin. The rostral-hypostomal plate (Pl. 1, figs 3–4, 6) was shield-shaped, the middle body of the hypostome convex, divided by a middle furrow, the smaller posterior portion inflated. A low macula, smooth externally, lay adjacent to the inner end of the middle furrow. The lateral border of the hypostome was narrow and convex, and bore terrace ridges parallel to the margin, these ridges curving outward anteriorly, and continuous with ridges on the inner edge of the doublure. The posterior border of the hypostome is convex but is narrower and lower than the lateral border, and bears terrace ridges. The small anterior wing is steeply inclined, without a pit in the external surface and hence presumably there was no wing process. The connective suture appears not only to have bounded the rostral plate, but to have continued along the anterolateral edge of the anterior wing, separating it from the almost vertical inner edge of the doublure. The external surface of the rostral plate bears only a single terrace ridge situated close to the anterior margin, and hence is distinct from the adjacent doublure. The inner portion of the posterior cephalic border is transverse, and outside the fulcrum the posterior margin curves back into the broad base of the genal spine; this spine extends back so that the tip is level (tr.) with the terminal axial portion of the pygidium (Pl. 1, fig. 6).

The thorax has the last three of the seven segments progressively shorter, the axis narrowing. The articulating furrow deepens into a pit a short distance from the axial furrow, an apodeme in line (exs.) with that of the

occipital furrow. The pleura has a wide (tr.) horizontal inner portion, the fulcrum approximately in line (exs.) with the eye lobe, the outer portion of the pleura narrowing rapidly and prolonged by a thorn-like pleural spine; this spine slightly longer on successive segments. Reed (1899) portrayed a short median spine on each axial ring, perhaps based on an irregular infold caused by compaction (Pl. 1, fig. 1); there seems no evidence for such spines. The irregularly broken posterior edge of the inner portion of each pleura, and the posterior cephalic border, is underlain by the leading edge (an articulating flange) of the following segment, and there is a small facet in front of the base of the pleural spine.

The pygidium shows five axial rings and a short terminal portion, the six pairs of pleurae in a radial arrangement, spinose, the last pair directed exsagittally behind the axis. The interpleural division is faint in the first three segments, a strong fold behind the next two segments, a faint sagittal furrow behind the axis. The pleural furrows are relatively broad and deep. The longer fourth segment bears a pleural spine which is wide at the base and extends back far beyond the pygidial margin (Whittington 1992, pl. 66). The doublure of the pygidium (Pl. 1, fig. 5) is a narrow strip, gently convex ventrally, beneath the outermost portion of the pleural region, continuous with the ventral side of the pleural spines. It bears terrace ridges which run concentrically to the margin, the outer ones curving to continue inside the edges of the spines. Thus the base of each pleural spine is seen to have arisen from the entire width of the pleura.

Remarks. Shergold (1969, p. 18) described *O. reynoldsi* from the Middle Cambrian of Australia, and very similar material is known from beds of the same age in Siberia (e.g. *O. reynoldsiformis* in Tchernysheva 1962, pl. 1, figs 1–8) and Korea (Saito 1934, p. 232, pl. 27, figs 17–20).

Oryctocephalus burgessensis Resser, 1938*b*

Plate 1, figure 2; Plate 2, figures 1–7; Plate 4, figure 1

1938*b*   *Oryctocephalus burgessensis* Resser, p. 37.
1951   *Oryctocephalus matthewi* Rassetti, p. 195, pl. 26, figs 4–5.

Holotype: USNM 96487, Walcott quarry, Burgess Shale (Rasetti 1951, pl. 26, fig. 2).

Other material. GSC collections of 1966 and 1967, from levels between 5 and 14 ft (1·52 to 4·27 m) in the Walcott quarry (Whittington 1971, fig. 3). ROM 38613, 49963–4, from talus in the Walcott quarry.

Geological horizon. Middle Cambrian, Stephen Formation, *Bathyuriscus-Elrathina* Zone; Walcott quarry in *Ptychagnostus praecurrens* Zone (Robison 1976, p. 104; Conway Morris 1989, fig. 1).

Remarks. A single specimen from the Walcott quarry (Whittington 1992, pl. 66) is referred to *O. reynoldsi*. All other specimens from the same locality, loaned to me from the GSC and ROM collections, are here referred to *O. burgessensis*. They are distinguishable from *O. reynoldsi* (compare Pl. 1, figs 1 and 6, with Pl. 1, fig. 2) by the more rounded antero-lateral outline of the cephalon, by the slightly advanced genal spine, and shorter genal and fourth pygidial pleural spines. These characters were not mentioned by Rasetti (1951, p. 194, pl. 26, figs 1–3), who discriminated a second species, *O. matthewi* (Rasetti 1951, p. 195, pl. 26, figs 4–5), in material from the Walcott quarry. This latter species differed supposedly in its shorter pleural and pygidial spines, but I am unable to see such differences in the available sample, nor are they evident in Rasetti's illustrations.

The glabella of *O. burgessensis* shows the deep, round S1–3 pits, the S1 pair joined by a shallow furrow, a faint, small S4 pit anterolaterally (Pl. 2, fig. 2), and an apodemal pit at the distal end of the occipital furrow. A small median occipital tubercle is present close to the anterior margin of the ring. At the fulcrum the posterior border turns to be directed outward and forward, rather than transversely, the angle in the posterior margin obtuse. In some specimens (Pl. 2, fig. 2) this angle is a blunt, backwardly-directed projection. Distally the border runs into the base of the genal spine, which lies in a transverse line with S0. The tip of the genal spine lies in a transverse line with the fifth thoracic segment. The curved thorn-like pleural and pygidial spines show a progressive increase in length from the first thoracic to the fourth pygidial spine, the two pairs inside the fourth pair being shorter (Pl. 2, figs 2, 5–6). The fourth pygidial spine is broad, and, in some specimens, of

length (exs.) less than that of the pygidium (sag.), in others broader and longer. The small triangular facet of the outer portion of the pleural segments, situated in front of the base of the pleural spine, has been exposed in the second, third and seventh segments of the original of Plate 2, figures 1 and 4.

McNamara and Rudkin (1984, p. 171, fig. 13b) described a specimen collected from talus below the Walcott quarry, thought to reveal events during exuviation, because the free cheeks and rostral-hypostomal plate were inverted, directed backwards, and lying to the left of the cranidium and thoracopygon. Other such assemblages of exoskeletal sclerites, including an articulated exoskeleton, are shown in Plate 2, figures 1–7 and Plate 4, figure 1 and their arrangement is commented on. No trace of appendages is preserved in any of these specimens, although they were found in layers at the same levels as those yielding soft-bodied fossils such as *Marrella splendens* (Whittington 1971, fig. 5). It is thought (Whittington 1980, p. 129; Conway Morris 1986, p. 424) that the Burgess Shale fossils were buried after transport in a suspension of fine-grained sediment, many coming to rest, as the sediment settled, parallel to the bedding planes. Hence the arrangement of the sclerites in these specimens is not related to moult behaviour but to decay, transport and burial. Before transport, were they carcasses or exuviae (Whittington 1990, fig. 6) held together by the ventral cuticle and articulatory membranes? Partial decay before transport, weakening the links between sclerites, may account for separation of the cranidium and some thoracic segments from the rest of the exoskeleton, and events during transport caused the rotation and partial separation of other sclerites. Decay of the remaining soft parts must have taken place after burial. I incline to the view that most, if not all, these specimens were exuviae. On moulting, the facial and connective sutures would have opened to allow egress of the newly-moulted animal, the weakest link in the exuviae being that between the cranidium and first thoracic segment (Whittington 1990, p. 35). The elasticity of the ventral cuticle, however, may have brought the edges of the connective sutures back into juxtaposition. Hence, specimens such as the originals of Plate 2, figures 3, 6–7, and Plate 4, figure 1, may have been partially decayed exuviae before transport led to the loss of some sclerites and twisting of others. More complete assemblages of sclerites (Plate 2, figs 2, 5) may have been fresh exuviae before transport, or possibly carcasses.

Genus LANCASTRIA Kobayashi, 1935

Type species. Olenopsis roddyi Walcott, 1912.

Diagnosis. Glabella subparallel-sided, S1–4 pits present, shallow transverse furrow connects S1 pair; eye lobe on outer part of cheek; anterior margin of rostral-hypostomal plate wide, connective suture

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EXPLANATION OF PLATE 2

Figs 1–7. *Oryctocephalus burgessensis* Resser, 1938. Middle Cambrian, Burgess Shale, British Columbia, Canada. Different arrangements of exoskeletal sclerites chosen from examples found in Walcott quarry; see discussion in text and further example in Plate 4, figure 1. 1, 4, GSC 110749; level 10 ft 4–8 ins (3·15 to 3·25 m), Walcott quarry; 1, exoskeleton with free cheeks displaced, cranidium fractured; × 5; 4, enlargement of left side of thorax showing pleural facets (arrowed); × 10. 2, 5, GSC 110747; level 5 ft 5 ins to 6 ft 2 ins (1·65 to 1·88 m), Walcott quarry; 2, internal mould of articulated dorsal exoskeleton; × 5; 5, part of external mould showing complete fourth pleural spine of pygidium (arrowed) and narrow marginal band of doublure; × 5. 3, GSC 110750, cranidium missing, free cheeks and rostral-hypostomal plate linked together, inverted, backward-facing and lying above thoracic segments 1–5; level 10 ft 4–8 ins (3·15 to 3·25 m), Walcott quarry; × 5. 6, GSC 110748, cranidium missing, right free cheek and rostral-hypostomal plate inverted, left free cheek detached, both cheeks partly beneath segments 1–3; level 10 ft 4–8 ins (3·15 to 3·25 m), Walcott quarry; × 5. 7, GSC 110746, cranidium and anterior four thoracic segments missing, remainder of exoskeleton articulated and in original relation; level 5 ft 1–6 in (1·55 to 1·77 m), Walcott quarry; × 5. Photographed in reflected light, dorsal views.

PLATE 2
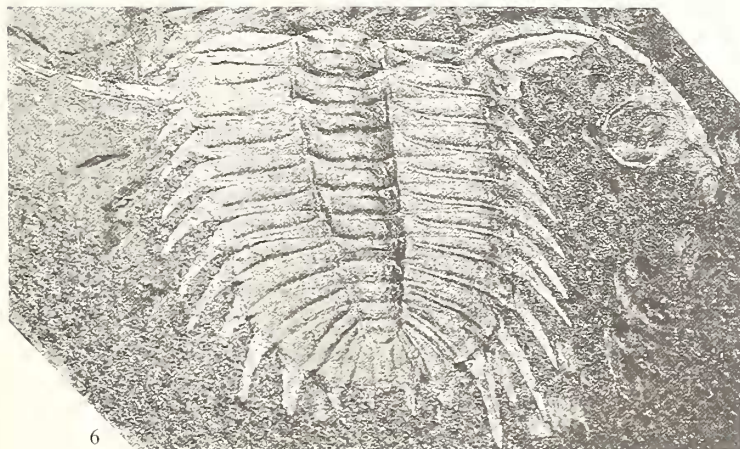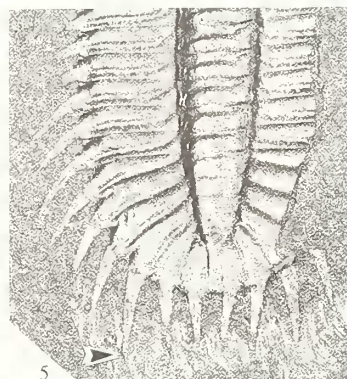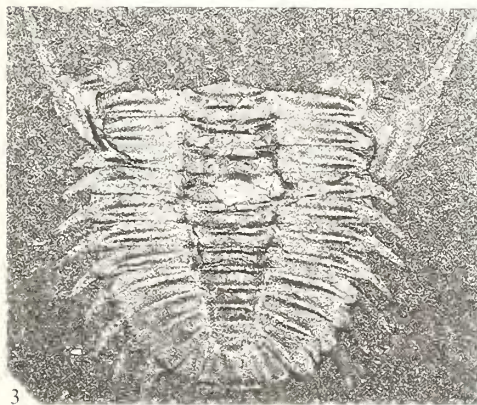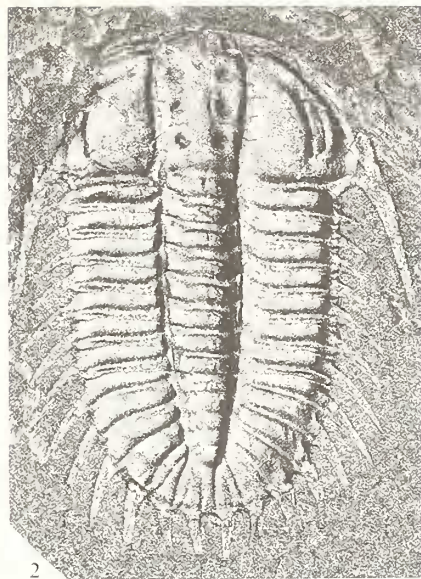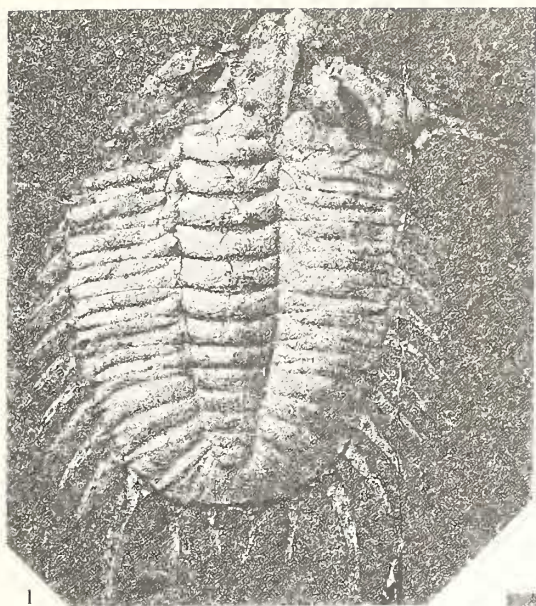
WHITTINGTON, *Oryctocephalus burgessensis*
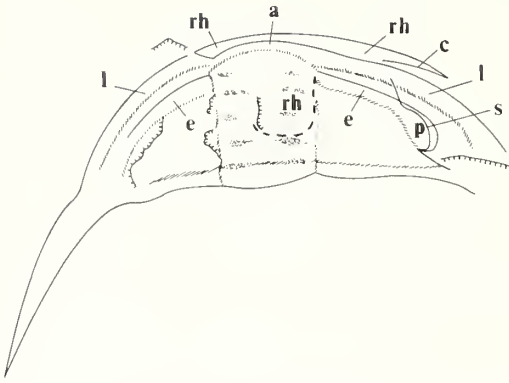
TEXT-FIG. 1. *Lancastria roddyi* (Walcott, 1912). An interpretation of what is preserved in the cephalon of the holotype (Pl. 3, fig. 2). a, anterior border; c, connective suture; e, eye ridge; l, lateral border; p, palpebral lobe; rh, rostral-hypostomal plate; s, facial suture. Hachures show break in slope; dashed line shows outline of hypostome. × 8·5.

directed strongly inward. Thorax may be non-fulcrate, of twelve segments, pygidium of four to eight segments.

Remarks. As indicated below, specimens from the Lower Cambrian in China, and the Middle Cambrian in Australia, show many similarities to the type species. *Goldfieldia*, known only from rare cranidia, was described from the Lower Cambrian of Nevada (Palmer 1964, p. 7, pl. 1, figs 14, 16–18) and recognized in the early Middle Cambrian of Antarctica (Palmer and Gatehouse 1972, p. 20, pl. 3, figs 7–8). It has the glabella expanding forward, with S1–4 and a small depression at the anterior margin; the anterior border is narrow, the fixed cheek wide. In these latter characters it resembles *Lancastria*. The cranidium described from the Lower Cambrian of northwestern Canada (Fritz 1972, p. 37, pl. 19, figs 20–21) appears to be of a similar type.

Oryctocephalops frischenfeldi Lermontova, 1940 (*in* Vologdin 1940, p. 137, pl. 42, figs 1, 1a–c); Tchernysheva 1962 (p. 42, pl. 3, figs 11–14); Suvorova 1964 (p. 246, pl. 28, figs 1–11; pl. 29, figs 1–7, text-figs 73–74) is from the Middle Cambrian, lower Amgan Stage, of the northern and eastern Siberian platform. This species is like *L. roddyi*, but the glabella expands forward slightly; both species may have twelve thoracic segments and the thorax of *O. frischenfeldi* appears to be non-fulcrate; the pygidium of the latter has only two segments. Suvorova described developmental stages of the meraspid cranidium, which in the earliest stage had long intergenal spines. A rounded projection from the posterior border of the holaspid is the remnant of this spine. Outside this projection the posterior border is directed outward and forward, so that the genal spine is slightly advanced.

Lancastria roddyi (Walcott, 1912)

Plate 3, figures 1–5; Text-figure 1

Holotype. USNM 58363, counterpart moulds in shale, quarry just west of Fruitville (the name 'Fruitvale' is an error), 2 miles (3·2 km) north of Lancaster, Lancaster County, Pennsylvania.

Other material. FM PA 89A, B, counterpart moulds of an incomplete exoskeleton, half a mile (800 m) south

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EXPLANATION OF PLATE 3

Figs 1–5. *Lancastria roddyi* (Walcott, 1912). Lower Cambrian, Kinzers Formation, *Olenellus* Zone, Pennsylvania, USA. 1, 4, FM PA 89, half mile (800 m) south of East Petersburg, Lancaster County; 1, latex cast of external mould, dorsal view; × 6; 4, internal mould, dorsal view, arrow indicates possible division between thorax and pygidium; × 6. 2, 5, USNM 58363, holotype, Fruitville, north of Lancaster; 2, internal mould, dorsal view, arrow indicates possible division between thorax and pygidium; × 5; 5, latex cast of external mould, dorsal view, tip of arrow on posterior border of cephalon; × 5. 3, FM PA 90, cranidium, latex cast of external mould, dorsal view; Donnerville, Lancaster County; × 7.

PLATE 3

WHITTINGTON, *Lancastria roddyi*

of East Petersburg, Lancaster County, Pennsylvania. FM PA 90, external mould of cranidium, Donnerville Quarry, Lancaster County, Pennsylvania.

Geological horizon. Lower Cambrian, Kinzers Formation, Lower Member, *Wanneria walcottanus* faunule (Campbell and Kauffman 1969), *Olenellus* Zone. In the block containing the holotype is a cephalon, and a small holaspid (with fifteen thoracic segments and the median spine) of *Olenellus* (*Paedeumias*) *transitans sensu* Palmer and Repina (1993, p. 22).

Description. The subparallel-sided glabella is divided by a straight occipital furrow (SO) and the pits S1–4, SO and S1–3 equally spaced from each other and the posterior margin, L4 and the anterior glabellar lobe successively slightly shorter (sag. and exs.) than LO–3. An apodemal pit is situated close to the outer end of the SO, the pits of S1–3 situated a short distance in from the axial furrow, the S1 pair connected by a shallow furrow; S4 is a shallower and smaller pit than S1–3, and is situated closer to the axial furrow. Long, curved eye lobe situated close to the lateral and posterior borders, anterior margin in transverse line with L3; palpebral lobe rises steeply from convex cheek. Prominent eye ridge directed inward and forward to axial furrow opposite L4. Anterior border narrow (sag.), convex, widening in front of the axial furrow and merging with the convex lateral border. Broad, shallow depression, the outer portion of the genal field, separates eye lobe and eye ridge from lateral border. Both the depth of this depression, and the convexity of the lateral cephalic border, appear to have been exaggerated by crushing (especially on the left side) of the holotype. Posterior border narrow (exs.), convex, border furrow well-defined; the lateral and posterior borders merging into the broad base of the genal spine, which tapers rapidly, the tip opposite the fifth thoracic segment. Anterior branch of suture curves forward and slightly inward, on to the lateral border; posterior branch of suture directed straight outward and backward. My interpretation of the holotype (Text-fig. 1) is that the rostral-hypostomal plate is partially preserved, displaced to the right and slightly in front of the cranidium. The rostral plate portion was broad (tr.), bounded by a strongly-inwardly directed connective suture. The concave impression on the mid-right of the glabella is part of the hypostomal portion, an external mould which shows a narrow, convex lateral border.

The thorax and pygidium in the holotype (Pl. 3, figs 2, 5) are of nineteen axial rings and pleurae and have a small terminal axial portion. Behind this terminal portion is a short (sag. and exs.) convex area, which bears a pair of short, backwardly-directed spines. A shallow sagittal groove separates these spines; it appears not to be a single plate as interpreted by Shergold (1969, p. 47, text-fig. 16A). Axial rings of uniform length (sag. and exs.), this length reduced progressively posteriorly, narrow (sag. and exs.), articulating furrow with shallow apodemal pit distally, faint lateral inflation of each axial ring, deep pit of articulating process in axial furrow. Pleurae (exclusive of spines), widest at first segment, decreasing progressively in width (tr.) and becoming more strongly backwardly directed, the last pair directed exsagittally. The pleural furrow curves back from the axial furrow, and is then directed slightly obliquely across the pleura. Pleural spines short anteriorly, those of segments 7–16 subequal in length, progressively more backwardly directed, by segment 15 slightly inward, spines of segments 17–19 shorter, the pair behind the terminal piece shortest. A second specimen (Pl. 3, figs 1, 4) has the thorax and pygidium displaced slightly and rotated to the right behind segment 7, and on the left shows 16 segments and the short (sag.) terminal axial piece. The terminal piece bears a pair of short spines. Walcott (1912, p. 245) and Shergold (1969, p. 47) regarded the thorax of the holotype as of nineteen segments, and the terminal piece as the pygidium. Admittedly it is difficult to detect a clear division between thorax and pygidium, but the broken rings of the axis show traces of the articulating half ring beneath the occipital ring and segments 1–12, but no farther posteriorly. Across the doublures of the pleural spines divisions between segments may be seen on segments 6–12, but not farther backward. I conclude that in the holotype the anterior twelve segments composed the thorax, and that the pygidium included seven segments and the terminal piece. The axis in the second specimen shows faint traces of articulating half rings, but clear divisions may be seen on the left side between segments 6–12, suggesting a thorax of twelve segments and a pygidium of four segments and the terminal piece.

In these two flattened specimens the anterior margin of each pleura passes below the edge of the segment in front to form an articulating flange, but there is no evidence of the fulcrum or a fulcral process. I consider it probable that the thorax was non-fulcrate.

An additional specimen (Pl. 3, fig. 3) appears to be that of an incomplete cranidium, showing the pits of S1–3, palpebral lobe and eye ridge, and posterior border.

Remarks. This species is very rare in the Kinzers Formation (Campbell and Kauffman 1969), and unknown elsewhere in North America. The holotype of *Oryctocephalina lancastrioides* Shergold, 1969 (pl. 11, fig. 1), from the Middle Cambrian of central Australia, is similar to that of *L. roddyi*,

especially if the latter has been shortened (sag. and exs.) by distortion. Shergold's holotype has the mould of the rostral-hypostomal plate (the hypostomal portion with a narrow, convex border) in place beneath the glabella. His enlargement (1969, p. 12, fig. 4) shows the impression of the inwardly directed connective suture of the rostral portion beneath the cephalic border, indicating that this rostral portion was wide (tr.). Shergold (1969, pp. 48, 51) preferred to refer his species to *Oryctocephalina*, but I consider it more probable that the species *lancastrioides* should be placed in *Lancastria*.

A species from the Lower Cambrian of China, *Changaspis placenta* (Zhang *et al.* 1980, pl. 89, fig. 11; pl. 90, figs 1–5) is like *Lancastria roddyi* in glabellar lobation, position of eye lobe, and narrow, convex cephalic border; the thoracopygon in the two species is also similar. The specimens of *C. placenta* show the wide (tr.) rostral plate fused to the shield-shaped hypostome, to form a rostral-hypostomal plate. Species of *Changaspis* are recorded from the Lower Cambrian of the Eastern Subprovince and Chiangnan Belt of the southwest China platform (Chang 1988, p. 55, chart 3), and from the Lower Cambrian of Greenland (Blaker 1986, p. 68, fig. 3).

Subfamily ORYCTOCARINAE Hupé, 1953

Diagnosis. Exoskeleton lacking genal spine and pleural spines on thorax or pygidium; facial suture opisthoparian, may be gonatoparian, and in *Ovatoryctocara* is proparian; thorax non-fulcrate in certain genera; granulate sculpture in many species.

Remarks. In the genera described or discussed below (*Oryctocara*, *Arthricocephalus* and its subgenera, *Sandoveria* and *Ovatoryctocara*) the rostral-hypostomal plate is unknown. However, the absence of a preglabellar field, and the glabella abutting against the narrow (sag. and exs.) anterior border, suggest that the hypostome was conterminant; it may have been fused to the rostral plate. Because the glabellar furrows are developed as pits it remains a reasonable assumption that these forms are oryctocephalids. They also have the characteristic pygidium, lacking a clearly defined border but having probably a narrow doublure.

In the Lower and Middle Cambrian of China many species of Oryctocarinae have been described, including those referred to *Feilongshania* (Zhang *et al.* 1980, p. 272, pl. 91, fig. 3) and *Duyunaspis* (Zhang *et al.* 1980, p. 273, pl. 91, figs 5–6). The type species of these two genera, from the Lower Cambrian, have a relatively much wider axial region than *Oryctocara*. The thorax in *Feilongshania* appears to be non-fulcrate, but in *Duyunaspis* the fulcrum appears to be situated at about half the width (tr.) of the pleura, the outer portion of which is facetted.

Genus ORYCTOCARA Walcott, 1908*b*

Type species. Oryctocara geikiei Walcott, 1908*b*.

Diagnosis. Axial region narrow, about one-quarter the width of the exoskeleton; glabella parallel sided, S1–3 deep, S4 shallow; eye lobe situated mid-way across cheek. Thorax of twelve segments, pygidium of seven segments; doublure narrow, convex.

Remarks. The type material of *Arthricocephalus chauveani* Bergeron, 1899, from the Lower Cambrian of Guizhou (Lane *et al.* 1988) shows that the glabella expands forward slightly; S1–4 are present, S1–3 connected by shallow transverse furrows; the eye lobe is shorter and farther out on the cheek than in *O. geikiei*; and the thorax is of eight segments. Lane *et al.* describe the thoracic pleurae as weakly geniculate, and facets may be present; these authors also describe a narrow pygidial border. In Lane *et al.* (1988, p. 1, fig. 5), a narrow groove forms the lateral and posterior margins of the pygidium; I regard this as the mould of a narrow doublure. Zhang *et al.* (1980) illustrate species of *Arthricocephlus* and *A.* (*Arthricocephalites*), which show (e.g. pl. 92, figs 1, 7–8; pl. 93, figs 2, 4) an apparently non-fulcrate thorax and the absence of a pygidial border. The claim (Lane *et al.* 1988) that the hypostome was subquadrate in outline and fused to the doublure

in *Arthricocephalus* is not substantiated by an illustration. *Arthricocephalus* occurs in the late Lower Cambrian of Greenland (Blaker 1986, p. 68, fig. 3; Lane *et al.* 1988, pl. 1, fig. 6); it may also be present in Siberia, if *Oryctocarella* is synonymous as Suvorova (1964, p. 235) suggested.

The Australian Middle Cambrian *Sandoveria lobata* Shergold, 1969 (p. 39, pl. 10, figs 1–11; text-figs 14–15) is distinguished from *Oryctocara* by the forwardly tapering glabella and seven thoracic segments. The glabella has the distinctive pre-occipital (or intervening in Shergold's terminology) lobe and additional rounded, lateral glabellar lobes are preserved in a meraspid cranidium (Shergold 1969, pl. 10, figs 7–8). Similar lateral lobes have been described in *Euarthricocephalus* from the Lower Cambrian of Zhejiang (Ju 1983). In *Sandoveria* S1–4 are present, S1–3 connected by transverse furrows: how far the connections of S1–4 to the axial furrows are real, or the result of flattening, is uncertain. The thoracic segments have the high, crescentic portion of the axial ring (overlying the articulating half ring) as in *Oryctocara*, the anterior and posterior margin of each flat pleura parallel, with no facet developed. The thorax is non-fulcrate, and the pygidium lacks a border.

In the early Middle Cambrian of Siberia species attributed to *Oryctocara* (Tchernysheva 1962, p. 36, pl. 5, fig. 5; Suvorova 1964, p. 236) have been described, and also species of *Ovatoryctocara* Tchernysheva, 1962. The type species *Oryctocara ovata* Tchernysheva, 1960 (p. 220, pl. 51, figs 4–6; proposed in Tchernysheva 1962, as a subgenus of *Oryctocara*) appears to be a distinct genus (Tchernysheva 1962, p. 37, pl. 4, figs 1–5; pl. 5, figs 1–4; Suvorova 1964, p. 242, pl. 27, fig. 17; text-fig. 72; Egorova *et al.* 1976, p. 96, pl. 46, figs 15–16; pl. 48, fig. 17) characterized by the proparian facial suture, the genal angle rounded and lacking a spine, four thoracic segments, the relatively long pygidium with ten to twelve axial rings and ten pleural ribs. The cheeks and pleurae are not granulate, but bear a network of fine ridges. Tchernysheva's illustrations also show that the thorax may have been fulcrate in *Ovatoryctocara*, the fulcrum at about the mid-width (tr.) of the pleura, and the pleura facetted. Two additional species of *Ovatoryctocara* are *O. angusta* and *O. granulata* (Tchernysheva 1962, p. 39, pl. 5, figs 6–12), the latter (Egorova *et al.* 1976, p. 96, pl. 43, figs 15–17) displaying granulate sculpture and a probably fulcrate thorax. *O. granulata* has been recorded (Robison *et al.* 1977, p. 261) but not described, from the late Lower Cambrian of south-eastern Newfoundland.

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Oryctocara geikiei Walcott, 1908*b*

Plate 4, figures 2–3, 4?, 5–9

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1908*b*   *Oryctocara geikiei* Walcott, pp. 23–26, pl. 1, figs 9–10.

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EXPLANATION OF PLATE 4

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Fig. 1. *Oryctocephalus burgessensis* Resser, 1938. Middle Cambrian, Burgess Shale, British Columbia, Canada. Arrangement of exoskeletal sclerites, cranidium missing, right free cheek inverted, rostral-hypostomal plate inverted, left free cheek not inverted (in relation to thoracopygon), both cheeks lie partially beneath segments 1 and 2, connective sutural margin of right cheek arrowed; GSC 110751, Walcott quarry, level 13–14 ft (3·96 to 4·27 m); × 5. Photographed in reflected light.

Figs 2–9. *Oryctocara geikiei* Walcott, 1908. Middle Cambrian. 2, USNM 95038, incomplete cranidium; Lakeview Limestone, *Peronopsis bonnerensis* Zone, cement mine just north of Lakeview, Pend Oreille Lake, Idaho, U.S.A.; × 10. 3, USNM 53427, external mould of pygidium and fragment of posterior thoracic segment; Spence Shale Formation, *P. bonnerensis* Zone, Liberty Canyon, west of Montpelier, Idaho; × 5. 4, USNM 95041 (Resser 1939*a*, p. 22), small pygidium doubtfully assigned to this species, horizon and locality as fig. 2; × 10. 5–6, lectotype, respectively USNM 53428, latex cast of external mould; USNM 53426, internal mould; locality and horizon as fig. 3; × 10. 7, 9, ROM 49460, respectively internal mould and latex cast of external mould; Stephen Formation, *Glossopleura* Zone, Mt Stephen, British Columbia, Canada; × 6. 8, ROM 49464, external mould, axial region compressed from occipital ring backward, locality and horizon as figs 7 and 9, × 6.

PLATE 4

WHITTINGTON, *Oryctocephalus, Oryctocara*
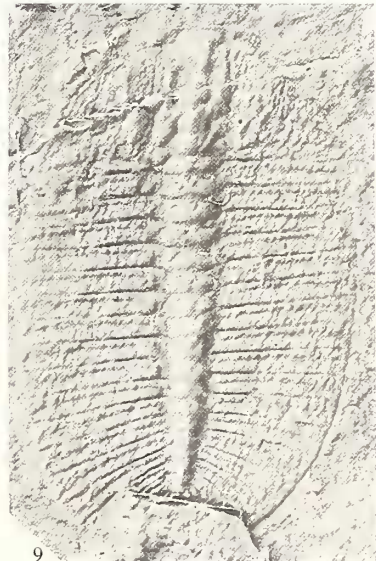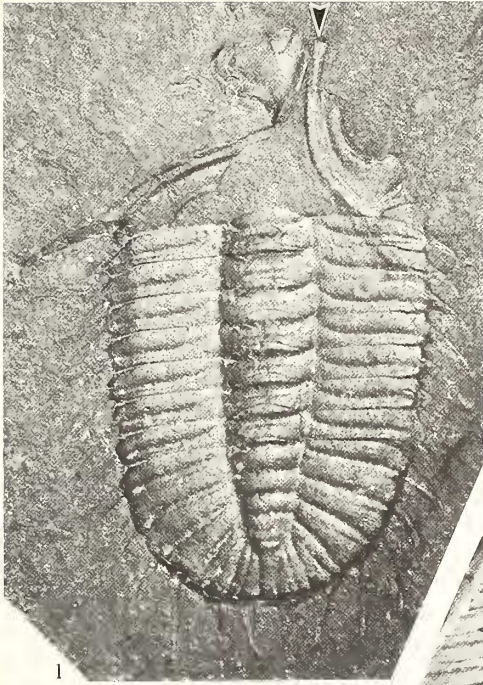
Lectotype (here selected). USNM 53426, 53428, counterpart moulds of incomplete, crumpled and partially disarticulated exoskeleton, original of Walcott 1908*b*, pl. 1, fig. 9; from the Spence Shale, in Spence Gulch, a ravine running up into Danish Flat from Mill Canyon, about 15 miles (9·37 km) west of Montpelier and 5 miles (3·12 km) southwest of Liberty, Bear Lake County, Idaho, USA.

Other material. USNM 53427, external mould of pygidium and fragments of posterior thoracic segments, original of Walcott 1908*b*, pl. 1, fig. 10, horizon and locality as lectotype. USNM 95038, external mould of incomplete cranidium, original of Resser 1938*a*, pl. 1, fig. 22, Lakeview Formation, southern side of Pend Oreille Lake, Bonner County, Idaho (referred to this species in Resser 1938*b*, p. 38; see Resser 1939*a*, p. 14). ROM 49459–61, Stephen Formation, Mt Stephen, locality 9 of Collins *et al.* 1983, the large block that also yielded *Sanctacaris uncata* (Briggs and Collins 1988). ROM 49464, Stephen Formation, beds immediately above locality 9 of Collins *et al.* 1983. ROM 49457–58 from steeply dipping, thin bedded siltstones, Stephen Formation, in a gully west of locality 9. ROM 49462–63, Stephen Formation, south-west shoulder of Mt Field, about 400 m south-west of the peak, at about 2400 m altitude.

Geological horizon. Middle Cambrian. The Spence Shale Formation (Robison 1991, p. 94) and the Lakeview Formation yield the fauna of the *Peronopsis bonnerensis* Zone (Robison 1976, p. 103), a zone equivalent to the upper *Albertella* and *Glossopleura* zones (Conway Morris 1989, fig. 1). All the ROM localities given above yielded *Glossopleura* sp., *Oryctocephalus* sp. and other trilobites indicative of the *Glossopleura* Zone, present in the basal portion of the Stephen Formation (Fritz 1971, p. 1164).

Description. Exoskeleton suboval in outline, maximum width at sixth thoracic segment, axis one-quarter or less of this width (tr.); no genal or pleural spines; pleurae transverse anteriorly, behind about the eighth thoracic segment progressively more strongly backwardly directed. Glabella subrectangular in outline; preglabellar field lacking; narrow (sag. and exs.) anterior border. Occipital ring short (sag. and exs.); occipital furrow with deep pit situated a short distance in from the axial furrow. S1–3 in form of deep rounded pits, situated at equal distances from each other and the occipital furrow, and a short distance inside the axial furrow; shallow transverse furrow connects S1 and S2 pits, fainter furrow connects S3 pits; anterior glabellar lobe about twice length (sag. and exs.) of L3, faint impression of S4 close to axial furrow at about midlength. Glabella abaxial to pits inflated, with incompletely defined, small, circular lateral lobe in front of extremity of occipital ring, and outside S1 pit; whether these lobes are real or the result of the flattening of the glabella is uncertain. Palpebral lobe a low ridge, gently curved and subparallel to axial furrow, situated at about one-third the width (tr. at the posterior margin) out from the axial furrow; anterior end of lobe opposite S4, posterior end opposite mid-L2. Faint eye ridge directed inward and forward to anterior extremity of axial furrow. In the original of Plate 4, figures 7 and 9, the cheeks are displaced inward, obscuring the palpebral lobe. However, the lateral border is partly preserved on the left side, is wider (exs.) than the anterior border, is of uniform width and meets the posterior border at an angle of *c.* 75°. Posterior border defined by forwardly curved border furrow so that it is longest (exs.) medially. Anterior branch of suture directed forward and slightly inward; posterior branch curves outward and backward to cross border close inside genal angle.

The lectotype (Pl. 4, figs 5–6) shows eleven thoracic segments disarticulated from the cranidium, and the pygidium and at least one segment detached and lying behind them. In articulated specimens (Pl. 4 figs 7–9) there appear to be twelve thoracic segments, the interpleural furrows of the pygidium dying out before they reach the margin. A broad (sag. and exs.) articulating furrow separates a narrow, convex axial ring from the strongly convex articulating half ring; apodeme close to the extremity of the articulating furrow. A depression at the posterior margin of the axial furrow is formed at the axial articulating process. The flat pleura shows no evidence of the fulcrum; it is divided by a shallow pleural furrow which curves forward from the axial furrow, is then directed straight outward, to die out just inside the margin. Posterior band longer (exs.) than anterior; narrow marginal band (an articulating flange) lies in front of anterior pleural band and fits below margin of pleura in front. At the extremity pleura is smooth, the margin truncated exsagittally and gently bent down. The anterior and posterior margins of each pleura are parallel, and there is no facet at the anterolateral angle. On the right side of an internal mould (Pl. 4, fig. 7) a groove extends continuously along the edges of the pleurae and pygidium (a corresponding ridge in the external mould). I interpret this structure as the narrow (tr.), convex doublure of pleurae and pygidium.

The subsemicircular pygidium (Pl. 4, figs 3, 7) has six pleural furrows and the shallower, narrower interpleural grooves curving outward and back, the posterior pair directed straight back (exs.) from each side of the sixth axial ring, and enclosing a tiny terminal axial piece and the faint indications of a seventh pleural

pair. Pleural, and especially interpleural, furrows extend out close to the bent-down exoskeletal margin, and there appears to have been a narrow, convex doublure. There was thus no smooth or raised border on the pygidium, and no border furrow.

External surface sculptured with closely-packed granules, most prominent on the genal field and pleural region, less so on the axial region (particularly the glabella), and absent in the furrows.

Remarks. The incomplete cranidium (Pl. 4, fig. 2) from the Lakeview Formation appears to belong to this species. An internal mould of a pygidium (Pl. 4, fig. 4) also from the Lakeview Formation, Pend Oreille Lake, is half the size of that of the lectotype, but may represent this species. It has six axial rings and the terminal axial piece, and six pairs of pleurae, with the pleural furrows deep, and is granulate on the anterior and posterior bands.

Addendum. Since this manuscript was completed, F. A. Sundberg (1994, Corynexochida and Ptychopariida (Trilobita, Arthropoda) of the *Ehmaniella* Biozone (Middle Cambrian), Utah and Nevada. *Contributions in Science, Natural History Museum of Los Angeles County*, **446**, 1–137, 93 figs) has described the new genus and species *Opsiosoryctocephalus ophis* and two species of *Tonkinella*. The former is based on small, silicified cranidia, a free cheek bearing a genal spine, and pygidia with marginal pleural spines. The material of *Tonkinella* includes cranidia and pygidia, and is preserved in relief. These species all come from the *Ptychagnostus gibbus* Zone.

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